CHAPTER 12:
SINGLE-SPECIES RELATIONSHIPS IN LOTIC AND LENTIC RIPARIAN ECOSYSTEMS

INTRODUCTION

A few individual species of special interest are addressed in this chapter. The management of lakes and streams in the Lake Tahoe basin typically focuses on recreation and sediment management. To date, basin specific information on the habitat relationships of riparian, meadow, and aquatic species (other than fish) has been sparse. The brown-headed cowbird poses unique risk to the viability of riparian associated bird species, specifically the many cup-nesters that comprise the majority of the nesting songbirds in riparian habitats in the basin. The habitat requirements and locations of frogs and toads were of particular interest in the basin, based on their relative rarity and declining trends in the Sierra Nevada and elsewhere. Beavers are of particular interest because of their ability to have substantial influence on channel morphology in lotic ecosystems. Waterfowl are also of interest; however, they were addressed as a group in the Chapters 4 and 11. The issues associated with each species addressed in this chapter are discussed in more detail below.

Brown-headed Cowbird

The Brown-headed Cowbird is of special interest in this study because of the effects it may have on the basin's songbirds in riparian and meadow ecosystems. The cowbird is a generalist parasite; it lays its eggs in the nests of other species and allows the host species to hatch and rear the cowbird's young (Brittingham and Temple 1983, Ehrlich et al. 1988). Thus, the cowbird does not build a nest of its own. Because cowbird eggs usually hatch 1 day prior to those of the host brood, chicks develop rapidly and are able to dominate food provisions at the expense of the host brood. Furthermore, cowbirds often eject eggs of host species when they lay their own (Robinson et al. 1993). Ehrlich et al. (1988) reported that as many as 144 North American bird species are vulnerable to reduced reproductive success as a result of brown-headed cowbird brood parasitism, particularly flycatchers, vireos, warblers, tanagers, and thrushes (Brittingham and Temple 1983). In the basin, several species of concern are susceptible to parasitism, such as the Willow Flycatcher and Yellow Warbler (Schlesinger and Holst 2000).

The effect of cowbird parasitism is not equal among passerine species because many host species have developed the ability to recognize and reject cowbird eggs. This ability is most likely dependent on the amount of time that cowbird and host species have co-occurred (Ehrlich et al. 1988). Thus, because cowbirds have only recently expanded their range into the Lake Tahoe basin (Orr and Moffitt 1971), passerine species in the basin are probably extremely vulnerable to reproductive failure due to nest parasitism.

Cowbird habitat relationships have been well studied. Wilcove et al. (1986) noted that cowbirds historically were associated with grazing mammals of grasslands because insects were readily available. In the Lake Tahoe basin, grazing mammals occur in open habitats adjacent to forest habitats. Additionally, forest habitats in the Lake Tahoe basin have been converted to more open environments such as golf courses and playing fields. Human habitat edges resulting from development tend to be more abrupt and prevalent than naturally occurring ecotones and can increase cowbird parasitism due to the accessibility of the forest interior. Gates and Gysel (1978) found that cowbird parasitism was a primary cause of mortality in passerine species along the ecotone between field and forest habitats in Michigan. Increases in habitat edges can facilitate parasitism by cowbirds, resulting in increased songbird mortality (Brittingham and Temple 1983).

Documenting cowbird occurrence and habitat use is an important first step in determining whether intervention is warranted (Robinson et al. 1993).

Beaver

Beaver is an exotic species in the Lake Tahoe basin. The beaver is considered to be an ecosystem engineer by some authors (e.g., Lawton and Jones 1995). The beaver is of special interest in the Lake Tahoe basin because of the significant structural changes they can and have induced in many stream systems within the basin. Beaver detections were obtained from riparian and channel searches. We describe reach and watershed characteristics where beaver were observed in the interest of better understanding the distribution and environmental relationships of beaver in the Lake Tahoe basin.

Amphibians

Concern exists about amphibians in the Sierra Nevada (Drost and Fellers 1996, Knapp and Matthews 2000, USDA 2000) and in the Lake Tahoe basin (Manley et al. 2000). In addition to the 5 species known to occur in the basin (see Chapter 1), several other species may occur. Northern leopard frogs (*R. pipens*) occurred historically in the basin, but have not been seen in recent years (Jennings and Hayes 1994). In addition, 1 record of Yosemite toads (*Bufo canorus*) from Desolation Wilderness exists, but that observation was likely a misidentified western toad (Jennings and Hayes 1994). Finally, in summer 2000 there was a sighting of a California newt (*Taricha torosa*).

Six amphibians were identified as focal species in the *Lake Tahoe Watershed Assessment* (Manley et al. 2000), indicating that each merits conservation attention. The long-toed salamander has declined in some areas (Jennings 1996), little is known about the salamander's natural history in alpine environments (Tyler et al. 1998), and its life history makes it vulnerable to disturbance (Manley et al. 2000). Mountain yellow-legged frogs and Yosemite toads are California species of special concern (Jennings and Hayes 1994) and USDA Forest Service sensitive species (USDA 1998), and the US Fish and Wildlife Service is reviewing the status of both species to determine whether federal listing may be warranted. Even Pacific treefrogs and western toads, relatively common throughout the state, appear to have declined in the Sierra Nevada (Martin unpublished manuscript 1992, Drost and Fellers 1996). Bullfrogs and probably northern leopard frogs were introduced to the basin (Zeiner et al. 1988, Jennings and Hayes 1994) and bullfrogs in particular have been implicated in the decline of some frog species in California (Moyle 1973, but see Hayes and Jennings 1986). In addition, the northern leopard frog is a USDA Forest Service sensitive species (USDA 1998). It is therefore evident that for various reasons, all native amphibians in the Lake Tahoe basin may be at risk of population decline; furthermore, information about the distributions and environmental relationships of the exotic species will benefit efforts to manage them.

Long-toed Salamander

Long-toed salamanders are the only salamanders confirmed to breed in the Lake Tahoe basin. They breed chiefly in temporary ponds at low elevations and in permanent fishless ponds at higher elevations (Basey and Sinclear 1980, B. Shaffer, pers. comm., K. Leyse pers. comm.). Adults spend most of the year underground (Anderson 1967). Larvae appear especially vulnerable to predation by trout (Jennings 1996, Tyler et al. 1998). Individuals may remain in the larval stage over the winter (Kezer and Farner 1955), perhaps accounting for their susceptibility to trout predation. Kezer and Farner (1955) showed that elevation and lake area affected the timing of metamorphosis of long-toed salamanders. In addition, larval salamanders appear to be more common with high aquatic macroinvertebrate density (Tyler et al. 1998). No information is available on effects of human disturbance.

Pacific Treefrog

The Pacific treefrog is the most widespread amphibian in California, occurring in a variety of habitats from sea level to 3,300 m (Morey 1988a). It breeds in wet meadows, large lakes, small ponds, and slow-moving streams (Stebbins 1985), though temporary ponds are preferred breeding sites (Morey 1988a). Lake depth does not seem to be related to Pacific treefrog occurrence, apart from Bradford's (1989) observed minimum depth of 0.3 m. Munger et al. (1998) found that sites with treefrogs had more silt and emergent vegetation than sites without treefrogs. Bradford (1989) found that introduced trout fish and treefrog tadpoles tended not to coexist in the same lake, but the degree to which trout prey on treefrogs is unknown. Human disturbance does not seem to affect treefrogs to the degree that it affects other amphibians; treefrogs often occur at sites with considerable human visitation (pers. obs.).

Western Toad

Western toads, like Pacific treefrogs, breed in diverse habitats over a large elevational range (Stebbins 1985). Populations appear to be in decline in California's Central Valley (Fisher and Shaffer 1996) and in the Sierra Nevada (Drost and Fellers 1996). The reasons for decline remain unclear. Though toads are mostly protected from predators as adults by their poisonous parotoid glands, they are vulnerable to many predators as tadpoles (Morey 1988b). Little information exists on whether introduced fish prey on tadpoles and whether human disturbance has direct effects on toads.

Mountain Yellow-legged Frog

Mountain yellow-legged frogs perhaps have received the most attention of any Sierran amphibian in recent years. The disappearance of mountain yellow-legged frogs from much of their former range (e.g., Drost and Fellers 1996) has caused concern among herpetologists working in the region, in particular because much of the decline has occurred in seemingly pristine alpine environments. Mountain yellow-legged frogs breed primarily in lakes, meadows, and streams above 1365 m and are aquatic throughout their life cycle. They tend not to co-occur with trout (Bradford 1989, Knapp and Matthews 2000), which prey on the frog in all life stages (Bradford 1989). Mountain yellow-legged frog tadpoles live for at least 1, and perhaps 2 winters before metamorphosing into adults; some researchers have hypothesized that the extended period in the larval stage makes them especially vulnerable to predators (Bradford et al. 1993). Introduced salmonids may have had a large impact on mountain yellow-legged frogs, possibly wiping out entire populations in some areas (Knapp and Matthews 2000). Banta (1965) and Morey (1988c) noted the mountain yellow-legged frog as occurring in the Lake Tahoe basin, but information on specific breeding sites is scarce.

Bullfrog and Northern Leopard Frog

Bullfrogs were introduced to California in the late 1800s to replace diminishing populations of red-legged frogs, which were harvested for food (Hayes and Jennings 1986). Many researchers have hypothesized that predation by bullfrogs is responsible in part for the decline of native amphibians (e.g., Moyle 1973, but see Hayes and Jennings 1986), usually citing predation on native species. Bullfrog ranges have been expanding in recent years; elevations of 1830 m have been recorded (Morey 1988d). For now, however, bullfrogs have not invaded high-elevation wilderness areas (Morey 1988d). We expected to find bullfrogs only at high disturbance, low elevation sites in the Lake Tahoe basin. Whether northern leopard frogs in the Lake Tahoe basin are native or introduced is unclear; regardless, they have not been located in the basin in recent years (Jennings and Hayes 1994).

Garter Snakes

Three species of garter snakes comprise the aquatic reptile fauna of the Lake Tahoe basin: the common garter snake (*Thamnophis sirtalis*), the western terrestrial garter snake (*T. elegans*), and the western aquatic garter snake (*T. couchii*) (Zeiner et al. 1988). Garter snakes are poorly studied in the basin, and concern exists about their populations throughout the Sierra Nevada (G. Fellers pers. comm.).

Habitat relationships of the basin's garter snakes have not been well-studied. All 3 species in the basin occur primarily near water (Zeiner et al. 1988), despite differences in their common names. Garter snakes are predators of amphibians (Zeiner et al. 1988) and thus it may be informative to assess their distributions along with those of amphibians. In addition, some concern exists about the fate of garter snake populations (G. Fellers, pers. comm.) due to the decline of a major component of their prey base. In addition to amphibians, garter snakes also prey on fish and possibly insects (Stebbins 1985) and should be detected only where their prey occur. Garter snakes occupy various aquatic and terrestrial habitats (Fitch 1941), with only western terrestrial garter snakes occurring above 2400 m (8000 ft) (Zeiner et al. 1988).

METHODS

Methods of data collection and most analysis methods are in Chapter 3 for lotic ecosystems and Chapter 11 for lentic ecosystems. In short, the brown-headed cowbird was surveyed using point counts and time-area constrained searches. Amphibians and snakes were surveyed at lentic sites by walking the perimeter of lakes and meadows. Garter snakes were surveyed at lotic sites by a time-area constrained search. Beaver activity was surveyed using riparian search and watershed walk field methods (see Chapter 3). In the remainder of this section we describe analyses specific to single-species relationships.

For most species, we analyzed relationships of species' presence with environmental characteristics. For cowbirds and bullfrogs, species known to be associated with human disturbance, we also analyzed relationships with the road density index. We did not perform logistic regressions for any species whose frequency of occurrence was < 10% (n = 8).

We analyzed relationships of abundance for two species for which we had many detections: cowbirds and Pacific treefrogs. Cowbird abundance was calculated for each sample unit as the average number of cowbirds detected per point count, thereby eliminating potential biases associated with sampling effort. We analyzed the abundance of treefrogs using abundance classes. We created 3 categories of abundance, with more advanced age classes weighted more heavily than younger age classes. This method was used to approximate the increased survivorship of most amphibians with advancing age (Duellman and Trueb 1986). Counts of each age class (adults, subadults, larvae, and egg masses) were standardized for sampling effort by dividing counts by search time. Then, an abundance index was created using the following formula: $(8 \times \text{adults/min}) + (4 \times \text{subadults/min}) + (2 \times \text{larvae/min}) + \text{eggs/min}$. Finally, we examined the distribution of this abundance index for the most conspicuous break. Three categories were created: no treefrogs (0), low treefrog abundance (> 0 and < 1.5), and high treefrog abundance (≥ 1.5).

We analyzed environmental relationships of species' presence using logistic regressions. For logistic regressions, we used forward selection with the likelihood ratio criterion for variable inclusion. We analyzed environmental relationships of species' abundance using linear regressions. Regression methods are described in Chapters 3 and 11.

To test for potential impacts of fish on amphibian and garter snake distributions, we performed chi-square tests of independence. For taxa detected too infrequently for us to use chi-square tests (expected frequency of < 5 in any cell of the 2 x 2 contingency table), we report qualitative observations.

RESULTS

Brown-headed Cowbird in Lentic Riparian Ecosystems

General Patterns

Brown-headed Cowbirds were among the most frequent riparian–meadow birds detected, occurring at 28% of lentic sample units (Chapter 11, Fig. 87). Cowbirds ranged in abundance from 0 to 7 individuals per point count ($\bar{x} = 0.43$, SE = 0.11).

Environmental Relationships

Cowbird abundance was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 240). Cowbird abundance was positively related to littoral zone plant frequency, meadow vegetation, and the road density index. Cowbird abundance was negatively related to elevation, precipitation, slope, boulders, logs, deciduous–coniferous riparian, and subalpine conifer. Regression of abiotic environmental variables on average cowbird abundance resulted in a 3-variable model: negative associations with elevation, precipitation, and slope (adj. $R^2 = 0.245$; Table 241). Regression of sample unit variables on average cowbird abundance resulted in a 1-variable model: a negative association with boulders (adj. $R^2 = 0.038$; Table 241). Regression of vegetation variables on average cowbird abundance resulted in a 3-variable model: positive associations with aspen and meadow and a negative association with subalpine conifer (adj. $R^2 = 0.205$; Table 241). Backward stepwise regression on these 7 key variables resulted in a final 2 variable model: a positive association with meadow and a negative association with elevation ($F_{2,85} = 20.07$, $P < 0.001$, adj. $R^2 = 0.305$; Tables 241 & 242).

TABLE 240. Significant correlations of environmental variables with cowbird abundance at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Abiotic characteristics:		
Elevation	-0.433	<0.001
Precipitation	-0.430	<0.001
Percent slope	-0.402	<0.001
Sample unit characteristics:		
Boulders	-0.221	0.039
Vegetation characteristics:		
Littoral zone plant frequency	0.346	0.021
Logs	-0.269	0.011
Meadow	0.324	0.002
Deciduous–coniferous riparian	-0.196	0.068
Subalpine conifer	-0.252	0.018
Road density index	0.480	<0.001

TABLE 241. Variables selected in linear regressions of 3 groups of environmental variables and cowbird abundance. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variable	Cowbird abundance
Abiotic:	
Elevation	**N**
Precipitation	N
Percent slope	N
Sample unit characteristics:	
Boulders	N
Vegetation characteristics:	
Aspen	P
Meadow	**P**
Subalpine conifer	N
Variables in final model	*2*
Adjusted R^2	*0.305*

TABLE 242. Final regression model of key environmental variables related to average cowbird abundance at lentic sample units (n = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Meadow	2.158	0.528	0.366	4.081	< 0.001
Elevation	-0.182	0.035	-0.466	-5.195	< 0.001

The observed negative relationship between cowbird abundance and elevation could be influenced by disturbance at lower elevations. An analysis of covariance with elevation partitioned into 4 groups and road density index as a covariate showed that elevation was not significantly associated with cowbird abundance once the influence of disturbance was removed (Table 243).

TABLE 243. Analysis of covariance exploring the relationship between cowbird abundance and elevation with disturbance (road density) as a covariate. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin. SS = sum of squares; ν = degrees of freedom; MS = mean square.

Source of variation	SS	ν	MS	F	*P*
Within + residual	68.16	83	0.82		
Regression	5.99	1	5.99	7.30	0.008
Elevation	4.58	3	1.53	1.86	0.143
Model	26.35	4	6.59	8.02	<0.001
Total	94.50	87	1.09		

We examined scatter plots of cowbird abundance against the 2 environmental variables in the final regression model to elucidate potential environmental thresholds. Two potential thresholds related to elevation were evident: absence of cowbirds at sample units > 2600 m in elevation and < 2 cowbirds per point count at sample units > 2000 m in elevation (Fig. 96).

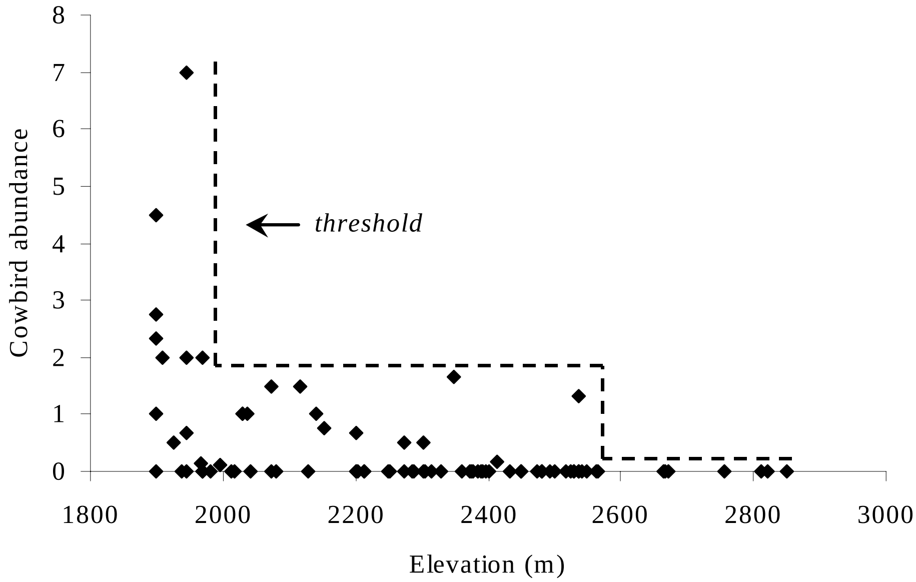

FIG. 96. Relationship of elevation to cowbird abundance at 88 lentic sample units in the Lake Tahoe basin. Cowbird abundance is measured as the number of birds per point count per unit.

Cowbird abundance was significantly positively related to road density index ($F_{1,86} = 25.74$, $P < 0.001$, adj. $R^2 = 0.221$; Table 244).

TABLE 244. Regression model of road density index and average cowbird abundance at lentic sample units ($n = 88$) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Road density index	0.431	0.085	0.480	5.074	< 0.001

Cowbird abundance was significantly different among basin orientations ($\chi^2_{KW} = 11.28$, d.f. = 4, $P = 0.010$), with the east side having significantly greater cowbird abundance than all other sides of the basin based on multiple comparison tests.

Brown-headed Cowbird in Lotic Riparian Ecosystems

General Patterns

Cowbirds were commonly detected, occurring at 62 (77.5%) of the 80 sample reaches. They ranged in abundance from 0 to 2.96 individuals ($\bar{x} = 0.83$, SE = 0.09).

Environmental Relationships

Brown-headed cowbirds were correlated with 15 of the 22 environmental variables (Table 245). Cowbird abundance was higher in association with greater sinuosity, lodgepole pine, meadow, alder-willow, and with west aspects. Conversely, cowbird abundance was lower in association with greater precipitation, elevation, channel gradient, distance to stream mouth, subalpine conifer, and woody debris.

Regression on biotic variables resulted in a 2 variable model: negative associations with elevation and precipitation (adj. $R^2 = 0.306$). Regression on channel variables resulted in a 3 variable model consisting of negative associations with channel width, gradient, and distance to mouth (adj. $R^2 = 0.320$). Regression on vegetation variables resulted in a 4 variable model: a positive association with alder-willow and a negative association with mixed conifer, subalpine conifer, and small logs (adj. $R^2 = 0.433$). Backwards step-wise regression on these 9 key variables resulted in a final 4 variable model, with brown-headed cowbird abundance increasing with an increasing proportion of alder-willow, and decreasing precipitation, channel gradient and small logs (adj. $R^2 = 0.560$) (Table 246). No thresholds were observed with the variables selected in the final model.

TABLE 245. Correlation and regression coefficients for brown-headed cowbird abundance in relation to 22 environmental variables. Data were collected at lotic riparian sample sites (n = 80) in the Lake Tahoe basin.

		Regressions (beta)	
Environmental variables	Correlations (r)	Individual regressions	Final regression
Abiotic environment:			
Elevation	-0.424****	-0.306***	
Precipitation	-0.487****	-0.398****	-0.484****
West aspect	0.243**		
East	-0.144		
North	-0.131		
South	0.029		
Channel characteristics:			
Width	-0.147	-0.252**	
Gradient	-0.422****	-0.493****	-0.385****
Sinuosity	0.193*		
Distance to mouth	-0.352***	-0.291***	
Vegetation characteristics:			
Mixed conifer	-0.036	-0.257**	
Subalpine conifer	-0.472****	-0.557****	
Lodgepole pine	0.229**		
Aspen-cottonwood	0.165		
Alder-willow	0.259**	0.204**	0.303***
Shrub	-0.097		
Meadow	0.358***		
Woody debris:			
Small log	-0.444****	-0.307***	-0.239***
Large logs	-0.390****		
Small snag	-0.229**		
Large snag	-0.352***		
Channel log volume	-0.122		

* $P \leq 0.10$; ** $P \leq 0.05$; *** $P \leq 0.01$; **** $P \leq 0.001$

TABLE 246. Final regression model of key environmental variables related to brown-headed cowbird abundance at sample reaches (n = 80) in the Lake Tahoe basin.

Variable	B	SE of B	Beta	T	*P*
Precipitation	-1.147	1.872	-0.484	-6.130	<0.001
Channel gradient	-0.426	0.087	-0.385	-4.900	<0.001
Alder-willow	1.333	0.332	0.303	4.018	<0.001
Small log	-0.105	0.036	-0.239	-2.926	0.005

Brown-headed cowbird abundance varied significantly among basin orientations (ν = 3, 76; SS = 5.88, 43.97; MS = 1.960, 0.579; F = 3.387; P = 0.022). Brown-headed cowbird abundance was greater on the east side compared to the west sides of the basin based on Tukey's test (P < 0.05).

Beaver

General Patterns

Beaver activity was observed in 11 of 20 watersheds. In over 50% (n = 6) of the 11 watersheds where beaver activity was observed, beaver activity was only observed on one of the 4 sample reaches. Of the remaining 5 watersheds, beaver activity was observed at 2 reaches in 4 watersheds and observed at 3 reaches in watershed. Beaver activity was never observed at all 4 reaches in a watershed.

Environmental Relationships of Beaver Presence

Beaver presence was correlated with 11 of the 22 environmental variables (Table 247). Positive relationships were observed with channel width, sinuosity, meadow vegetation, lodgepole pine vegetation, and channel log volume. Negative relationships were observed with elevation, west aspects, channel gradient, subalpine conifer vegetation, large log abundance, and canopy cover index.

TABLE 247. Significant ($P \leq 0.10$) correlations between beaver presence and 22 environmental variables. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin.

Environmental variable	Beaver presence	
	r	***P***
Abiotic environment:		
Elevation	-0.401	<0.001
West aspect	-0.225	0.045
Channel characteristics:		
Width	0.344	0.002
Gradient	-0.458	
Sinuosity	0.390	<0.001
Vegetation characteristics:		
Canopy cover index	-0.194	0.084
Subalpine conifer	-0.201	0.074
Meadow	0.292	0.009
Lodgepole pine	0.343	0.002
Large logs	-0.282	0.011
Channel wood volume	0.375	0.001

The logistic regression models for each environmental variable group were strong. The regression model for abiotic environment consisted of 2 variables: a positive association with precipitation and a negative association with elevation (correctly classified: presence = 41%, absence = 90%) (Table 248). The logistic regression model for channel characteristics consisted of 2 variables: a negative association with gradient and a positive association with width (correctly classified: presence = 47%, absence = 97%) (Table 248). Vegetation characteristics were separated into live vegetation and woody material for the beaver, since the beaver creates woody debris (versus woody debris being a component of beaver habitat). The logistic regression model for live vegetation consisted of 2 variables: a positive association with meadow and lodgepole pine (correctly classified: presence = 35%, absence = 95%) (Table 248). The prediction of presence was slightly improved by the inclusion of all 7 vegetation types (correctly classified: presence = 35%, absence = 95%). Backwards logistic regression on the 6 key variables (channel woody debris excluded) resulted in a 3 variable model: positive associations with meadow and precipitation; and negative associations with elevation (correctly classified: presence = 65%, absence = 95%) (Table 249).

TABLE 248. Regression relationships between beaver presence and 22 environmental variables at sample reaches (n = 80) in the Lake Tahoe basin. Environmental variables were transformed. N = negative association, P = positive association with $P \leq 0.10$.

Environmental variable	Beaver presence
Abiotic environment:	
Elevation	N
Precipitation	P
Channel characteristics:	
Width	P
Gradient	N
Vegetation characteristics:	
Lodgepole pine	P
Meadow	P
Large log	N
Channel wood volume	P

TABLE 249. Final logistic regression model for relationship between environmental variables and beaver presence. Data were collected on sample reaches (n = 80) in the Lake Tahoe basin.

Variable	B	SE	Wald	ν	P	R
Elevation	-27.140	8.365	10.527	1	0.001	-0.321
Precipitation	2.790	1.154	5.851	1	0.016	0.216
Meadow	2.165	0.994	4.747	1	0.029	0.182

The regression model for woody debris consisted of 2 variables: a positive association with channel woody debris and a negative association with large logs (correctly classified: presence = 41%, absence = 94%) (248). The inclusion of all 5 woody debris variables improved the prediction of presence (correctly classified: presence = 47%, absence = 92%).

I looked at individual relationships between beaver presence and each variable selected in the logistic regression models. Elevation averaged 1977 m (SE = 20.9) where beavers were present, and 2140 m (SE = 21.7) where beavers were absent. A 2-tailed t-test based on unequal variances showed that elevation was lower at reaches where beavers were present. ($P < 0.001$). Beaver was not observed above approximately 2200 m in elevation, although sample reaches ranged up to 2690 m in elevation (n = 18 > 2200m). Precipitation averaged 95.6 cm (SE = 7.71) where beavers were present, and 91.3 cm (SE = 4.47) where beavers were absent. A 2-tailed t-test based on unequal variances showed precipitation was not different between occupied and unoccupied sites.

Two channel variables, gradient and width, were selected in the step-wise logistic regression model. Gradient averaged 3.7% (SE = 1.28) where beavers were present, and 8.1% (SE = 0.65) where beavers were absent. A 2-tailed t-test based on unequal variances showed that gradient was lower where beavers were present (P = 0.003). Beaver was also not observed on sample reaches with channel gradients over 13%, although gradients ranged as high as 24% on some sample reaches. Average channel width where beavers were present was 7.91 m (SE = 1.22) compared to the average width of 4.26 m (SE = 0.44) where beavers were absent. A t-test based on unequal variances found that channel width was greater on reaches where beavers were present (P = 0.009). Beaver was not observed on streams less than 1.4 m wide (n = 3 < 1.4 m), and 80% of all detections were observed on streams greater than 2.5 m wide (n = 27 < 2.5 m). Sinuosity, the third channel variable but not selected by the logistic regression model, averaged 1.33 (SE = 0.087) where beavers were present, and 1.15 (SE = 0.012) where beavers were absent. A 2-tailed t-test based on equal variances found that sinuosity was greater on reaches where beavers were present (P = 0.001).

Two live vegetation variables, meadow and lodgepole pine, were selected in the logistic regression model. Meadow cover within the reach averaged 21.8% (SE = 6.7) where beavers were present, and 7.6% (SE = 2.3) where beavers were absent. A 2-tailed t-test based on unequal variances showed that meadow cover was greater where beavers were present. Lodgepole pine cover within the reach averaged 20.9% (SE = 5.9) where beavers were present, and 5.8% (SE = 2.2) where beavers were absent. A 2-tailed t-test based on unequal variances showed that lodgepole pine cover was greater where beavers were present.

Two woody debris variables, large logs and channel woody debris, were selected for the logistic regression model. Large logs averaged 113.7 m/ha (SE = 28.72) where beavers were present, and 158.2 m/ha (SE = 19.71) where beavers were absent. A 2-tailed t-test based on unequal variances showed that large logs were less abundant where beavers were present. Beaver was not observed on sample reaches with greater than approximately 1060 m/ha of large logs, although the large log density ranged as high as 2037 m/ha. Channel wood volume averaged 1093.3 m^3/ha (SE = 472.30) where beavers were present, and 418.9 m^3/ha (SE = 147.86) where beavers were absent. A 2-tailed t-test based on unequal variances showed that channel wood volume was higher, an average of almost 50% higher, where beavers were present.

Beaver activity was not detected on the north side of the basin, and ANOVA showed that beaver activity varied significantly among basin orientations ($F_{3,76}$ = 4.298, P = 0.007), and was significantly more frequent on the south side compared to the north side of the basin based on multiple comparison tests. Seventy-eight percent (n = 7) of the watersheds lacking beavers were on the north and east sides of the basin. A 2%2 Chi-square comparing the frequency of occurrence in watersheds on the north and east sides compared to those on the south or west sides of the basin showed a difference in frequency of occurrence than expected by chance (ν = 1, χ^2 = 5.50, P = 0.02), with beaver frequency of occurrence being greater on south and west sides of the basin.

A number of environmental variables varied with basin orientation in the Lake Tahoe basin, with channel width being the most likely of these parameters to limit beaver distribution. Beavers were present in 100% of the watersheds with an average channel width >5 m (Fig. 97), whereas they were present in only 39% of the watersheds with an average channel width of <5 m. In turn, channel width was highly correlated (r = 0.74) with watershed size (Fig. 98). Watershed size was significantly different (ν = 1,18, F = 4.91, P = 0.040) between watersheds occupied and unoccupied by beaver (Fig. 99), with beavers being more frequently present in larger watersheds. The largest watershed without beavers was Third Creek (1,544 ha), which is located on the north side of the basin, and the smallest watershed found with beavers was Glenbrook Creek (1,054 ha), which is located on the east side of the basin.

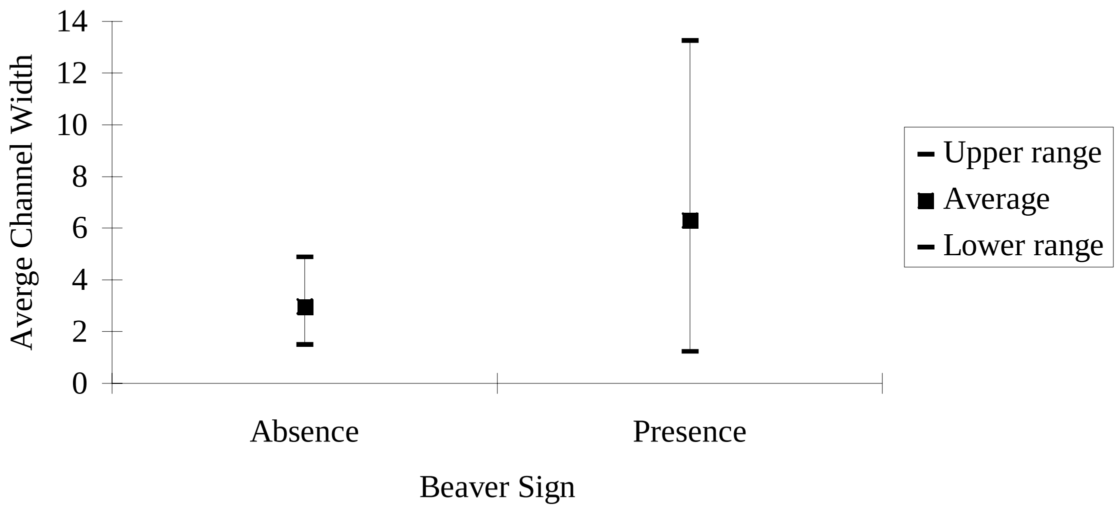

FIG. 97. Presence and absence of beaver sign by watershed in relation to average channel width of the watershed. Beavers were absent in 7 watersheds and present in 13 watersheds.

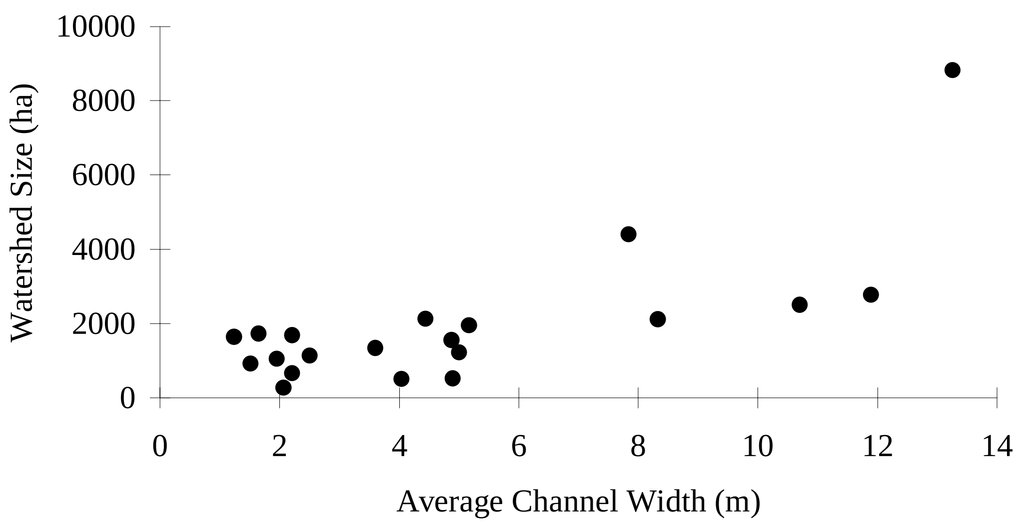

FIG. 98. Relationship between average channel width and watershed size for 80 sample reaches located in 20 watersheds in the Lake Tahoe basin.

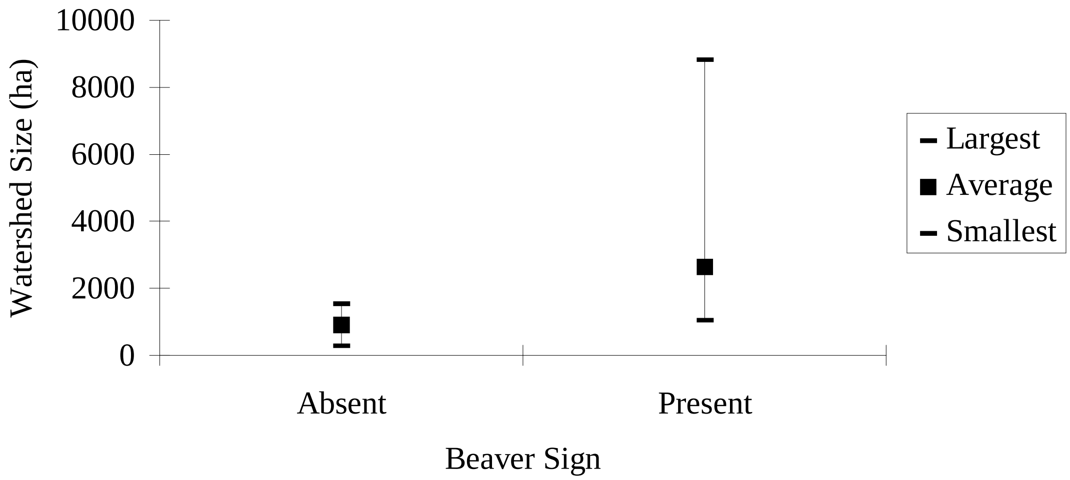

FIG. 99. Relationship between the presence of beaver and watershed size in 20 watersheds in the Lake Tahoe basin.

The strong associations with channel characteristics suggested that relationships may exist with channel type, a classification based on gradient and sinuosity (among other characteristics) and commonly used in land management planning. A multiple unplanned comparisons GT2 test was conducted to determine if particular channel types were associated with a greater frequency of occurrence of beavers. Based on all reaches (n = 80), a greater proportion of C-type channels were used by beavers in comparison to A-type channels. No other comparisons were significantly different. These results indicate beavers select high gradient channels less often than expected based on their availability.

Amphibians

General Patterns

Sampling detected all amphibian species (n = 5) known to be extant in the Lake Tahoe basin (Table 250). The Pacific treefrog was the most frequently occurring species, present at nearly 50% of sample units. The remaining species were present at only 1 to 8 sample units. The detection of long-toed salamanders at Edgewood Lake represents the first detection of a native salamander in Nevada (R. Espinoza, pers. comm.).

TABLE 250. Amphibian species detected at lentic sample units in the Lake Tahoe basin (n = 88).

Common name	Scientific name	No. units	Frequency (%)
Pacific treefrog	*Hyla regilla*	43	48.9
Western toad	*Bufo boreas*	8	9.1
Long-toed salamander	*Ambystoma macrodactylum*	6	6.8
Bullfrog	*Rana catesbeiana*	4	4.5
Mountain yellow-legged frog	*Rana muscosa*	1	1.1

Environmental Relationships of Pacific Treefrogs

Treefrog abundance was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 251). Regression of treefrog abundance on abiotic environmental variables resulted in no variables being selected. Regression of treefrog abundance on sample unit variables resulted in a 1-variable model: a negative association with depth (adj. $R^2 = 0.116$). Regression of treefrog abundance on vegetation variables resulted in a 1-variable model: a positive association with littoral zone plant diversity (adj. $R^2 = 0.056$). Backward stepwise regression on these 3 variables yielded the model with depth ($F_{1,86} = 12.43$, $P < 0.001$, adj. $R^2 = 0.116$) (Table 252).

TABLE 251. Significant correlations of Pacific treefrog abundance with environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Silt	0.281	0.008
Sand	-0.199	0.064
Cobbles	-0.326	0.002
Boulders	-0.275	0.010
Littoral zone plant diversity	0.236	0.027
Littoral zone plant frequency	0.235	0.028
Total macroinvertebrate abundance	0.293	0.006
Sample unit depth	-0.356	0.001
Mixed conifer	0.179	0.095

TABLE 252. Final regression model of key environmental variables related to Pacific treefrog abundance at lentic sample units (*n* = 88) in the Lake Tahoe basin. Beta = partial regression coefficient.

Variable	B	SE of B	Beta	T	*P*
Depth	-0.214	0.061	-0.355	-3.527	< 0.001

We examined scatter plots of depth against treefrog abundance to elucidate potential environmental thresholds. Two potential thresholds were evident. No treefrogs occurred at sample units > 13 m deep, and a no sample units > 4 m deep had a high abundance of treefrogs (Fig. 100).

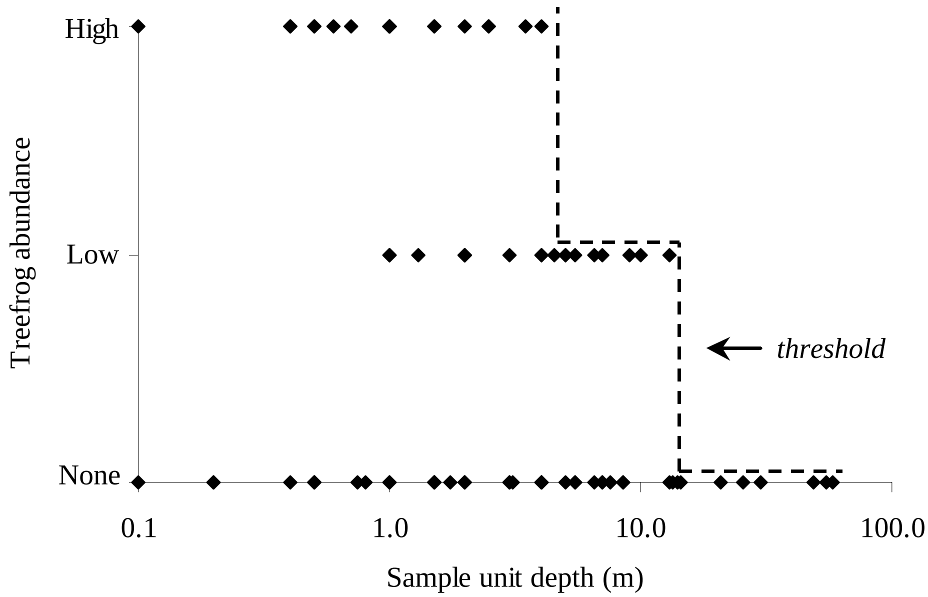

FIG. 100. Relationship of sample unit depth (plotted on a logarithmic scale) to treefrog abundance at 88 lentic sample units in the Lake Tahoe basin.

Treefrogs were present significantly less frequently at sample units with trout than at units without trout ($\chi^2_1 = 3.20$, $P = 0.074$; Fig. 101).

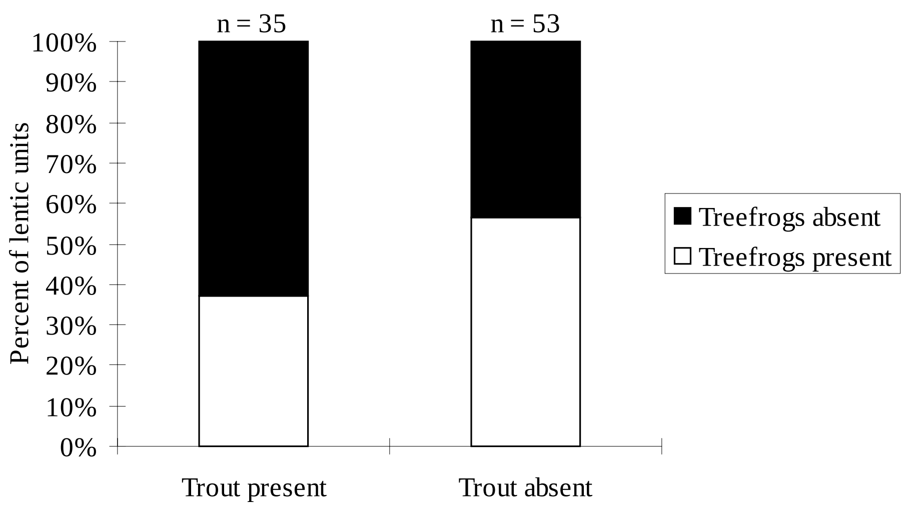

FIG. 101. Presence of Pacific treefrogs at sample units with and without trout present. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental Relationships of Western Toads

Western toad presence was significantly positively correlated ($P \leq 0.10$) with 3 environmental variables: area (r = 0.292, P = 0.006), slope (r = 0.178, P = 0.098), and subalpine conifer (r = 0.241, P = 0.024). Logistic regression of toad presence on abiotic environmental variables resulted in a 1-variable model: a positive association with slope (correctly classified: presence—0.00%, absence—100.00%). Logistic regression of toad presence on sample unit variables resulted in a 1-variable model: a positive association with area (correctly classified: presence—0.00%, absence—98.75%). Logistic regression of toad presence on vegetation variables resulted in a 1-variable model: a positive association with subalpine conifer (correctly classified: presence—0.00%, absence—100.00%). Backward stepwise regression on these 3 variables resulted in a 2-variable model that best predicted toad absence: positive associations with area and subalpine conifer (χ^2_2 = 14.00, P = 0.001, correctly classified: presence—12.50%, absence—100.00%; Table 253). No environmental thresholds for western toads were evident.

TABLE 253. Final logistic regression model of key environmental variables related to western toad presence at lentic sample units (n = 88) in the Lake Tahoe basin.

Variable	B	SE	Wald	df	sig	R	Exp(B)
Subalpine conifer	4.437	1.856	5.715	1	0.0168	0.263	84.503
Area	0.645	0.234	7.611	1	0.0058	0.324	1.905

Toads were not detected frequently enough for chi-square analyses to be performed (values of < 5 in more than 1 cell of the contingency table) to determine patterns of occurrence of toads relative to that of fish. Nonetheless, it appears that toads were more frequent at sample units where trout were present compared to where they were absent (Fig. 102).

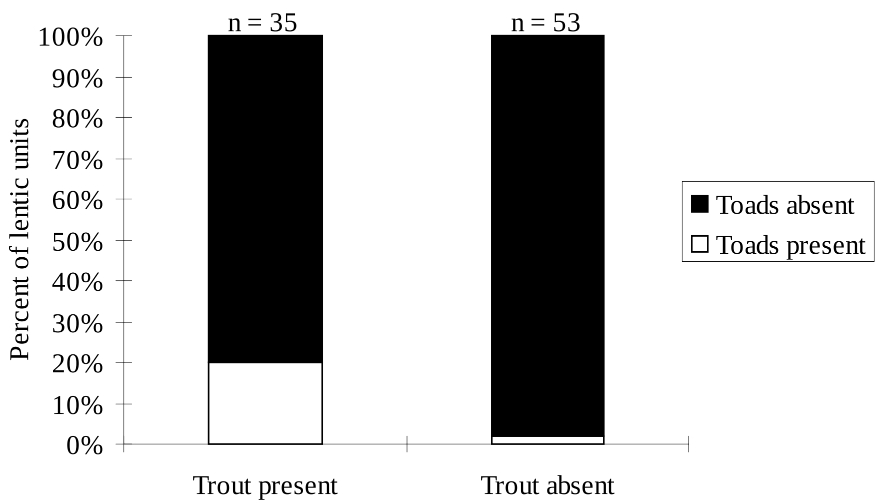

FIG. 102. Presence of western toads at sample units with and without trout present. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental Relationships of Long-toed Salamanders

Long-toed salamander presence was not significantly correlated with any environmental variables, and their low frequency of occurrence precluded any further analysis of their relationship with the environmental variables.

Salamanders were not detected frequently enough for chi-square analyses to be performed (values of < 5 in more than 1 cell of the contingency table) to determine patterns of occurrence of salamanders relative to occurrence of trout. Nonetheless, the data suggest that salamanders were less frequent at sample units where trout were present (Fig. 103).

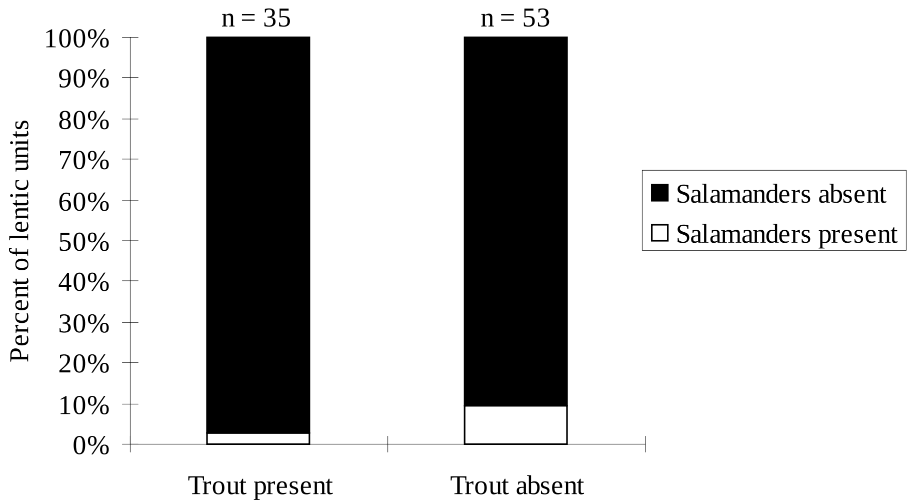

FIG. 103. Presence of long-toed salamanders at sample units with and without trout. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental Relationships of Bullfrogs

Bullfrog presence was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 254): decreasing presence at higher elevations and precipitations, a negative relationship with silt substrate, and positive relationships with sand and pebble substrates. Bullfrog presence was also positively correlated with the road density index (r = 0.293, P = 0.006).

TABLE 254. Significant correlations of bullfrog presence with environmental variables at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	r	*P*
Elevation	-0.276	0.009
Precipitation	-0.278	0.009
Silt	-0.222	0.038
Sand	0.210	0.049
Pebbles	0.235	0.027

Environmental thresholds for bullfrogs were observed but are speculative because of the low number of bullfrog detections: 1) bullfrogs were not detected at sample units above 2030 m in elevation, and 2) bullfrogs and other native amphibians were not detected together with the exception of a single sample unit (Seneca Pond) at which a low abundance of Pacific treefrogs was also detected.

Environmental Relationships of Mountain Yellow-legged Frogs

Mountain yellow-legged frogs were detected at only 1 of the 88 sample units; they were also detected at Hell Hole during an informal survey. Because of the high concern for this species and its apparent rarity in the basin, the 2 lentic units where it was encountered are described here.

Skinny Whale Pond is a 0.45-ha pond in Desolation Wilderness approximately 1 km east of Fontanillis Lake and 1 km north of Dicks Lake. A single 2^{nd}- or 3^{rd}-year tadpole and a single juvenile frog were detected. Other amphibians detected were Pacific treefrogs and long-toed salamanders. No fish were detected in the pond. The pond is approximately 2 m deep, and its substrate is composed of approximately 85% silt and 15% boulders, cobbles, and bedrock. Littoral zone vegetation occurred in 63% of transects, with an average littoral zone plant diversity of 0.7 species per transect. Primary vegetation types within 50 m of shoreline were wooded riparian (21%) and meadow (18%), with granite occupying the bulk of the surrounding area.

Hell Hole is a large wet meadow and *Sphagnum* bog complex near the headwaters of Trout Creek. Three 2nd- or 3rd-year tadpoles and 2 juvenile frogs were detected. Visits in subsequent years (1998 to 2000) have detected hundreds of tadpoles and as many as 3 adults. Other amphibians detected at Hell Hole were Pacific treefrogs and long-toed salamanders. No fish were present. The complex is approximately 1 km long and 100 m wide. Its depth is unknown, but several "pits" in the bog appear several meters deep. Hell Hole occurs on silt substrates, with a large buildup of peat in some places that creates a spongy mat, typical of bog ecosystems.

Amphibians by Basin Orientation

Pacific treefrogs were detected in all 3 abundance categories in all 4 basin orientations, but we were not able to perform a chi-square analysis of treefrog abundance by basin orientation (more than 1 cell of the contingency table had expected frequencies of < 5). Frequency of occurrence of treefrogs did not differ among orientations ($\chi^2_3 = 0.36$, $P = 0.947$). For the remaining amphibian species, too many cells had expected frequencies of < 5 for chi-square analyses to analyze the frequency of occurrence by basin orientation, but the following patterns were observed: long-toed salamanders were not detected on the north side, western toads were not detected on the south side, and bullfrogs were detected only on the south side.

Garter Snakes in Lentic Riparian Ecosystems

General Patterns

Garter snakes were present at 22.7% ($n = 20$) of sample units surveyed. We encountered all 3 species of garter snakes at sample units: common garter snakes, western aquatic garter snakes, and western terrestrial garter snakes. The frequency of occurrence of individual species was low, ranging from 3 sample units for the common garter snake to 9 sample units for the western terrestrial garter snake (Table 255). At only 2 sample units did we confirm the presence of 2 species of garter snakes.

TABLE 255. Garter snakes detected in surveys of lentic sample units ($n = 88$) in the Lake Tahoe basin.

Common name	Scientific name	Number of units	Frequency (%)
Common garter snake	*Thamnophis sirtalis*	3	3.4
Western aquatic garter snake	*Thamnophis couchii*	4	4.5
Western terrestrial garter snake	*Thamnophis elegans*	9	10.2
Unidentified garter snake	*Thamnophis* sp.	7	8.0
All garter snakes	*Thamnophis* spp.	20	22.7

Environmental Relationships of Garter Snakes

The presence of one or more species of garter snake was significantly correlated ($P \leq 0.10$) with several environmental variables (Table 256). Logistic regression of abiotic environmental variables on garter snake presence resulted in a 1-variable model: a positive association with precipitation (correctly classified: presence—0%, absence—100%; Table 257). Logistic regression of sample unit variables on garter snake presence resulted in a 2-variable model: positive associations with pebbles and depth (correctly classified: presence—25%, absence—94.12%; Table 257). The model's prediction of garter snake presence was improved by including area instead of depth (correctly classified: presence—35%, absence—94.12%). Logistic regression of vegetation variables on garter snake presence resulted in a 1-variable model: a positive association with logs (correctly classified: presence—0%, absence—100%; Table 257). Backward logistic regression on these 4 key variables resulted in a 3-variable model: positive associations with logs, pebbles, and area ($\chi^2_3 = 23.20$, $P < 0.001$, correctly classified: presence—40%, absence—94.12%; Tables 257 & 258).

TABLE 256. Significant correlations of environmental variables with garter snake presence at 88 lentic sample units in the Lake Tahoe basin.

Environmental variable	*Thamnophis* presence	
	r	*P*
Bedrock	0.258	0.015
Pebbles	0.353	0.001
Boulders	0.236	0.027
Cobbles	0.370	<0.001
Area	0.382	<0.001
Depth	0.402	<0.001
Precipitation	0.192	0.073
Logs	0.193	0.072
Silt	-0.225	0.035
Littoral zone plant frequency	-0.176	0.100
Aquatic invertebrate abundance	-0.229	0.032

TABLE 257. Variables selected in forward logistic regressions of 3 groups of environmental variables and garter snake presence. N = negative association and P = positive association at $P \leq 0.10$. Bolded = selected in the final regression at $P \leq 0.05$ on key variables from each group of environmental variables. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Environmental variables	Garter snake presence
Abiotic environment:	
Precipitation	P
Sample unit characteristics:	
Pebbles	**P**
Area	**P**
Vegetation characteristics:	
Logs	**P**
Variables in final model	*3*
Percent correctly classified	*81.82*

TABLE 258. Final logistic regression model of key environmental variables related to garter snake presence. Data were collected at lentic sample units (n = 88) in the Lake Tahoe basin.

Variable	B	se	Wald	ν	P	R
Logs	2.456	1.242	3.911	1	0.048	0.1423
Pebbles	3.257	1.399	5.419	1	0.020	0.1904
Area	0.494	0.166	8.902	1	0.003	0.2705

We examined scatter plots of garter snake presence against the 3 environmental variables in the final regression model to elucidate potential environmental thresholds. No thresholds were evident.

Garter snakes were detected only at sample units with either fish or Pacific treefrogs (Table 15). Garter snakes were significantly more frequent at sample units with trout than at sample units without trout (χ^2_1 = 9.87, P = 0.002; Table 259). Garter snakes were also significantly more frequent at sample units with minnows than at sample units without minnows (χ^2_1 = 8.57, P = 0.003). Garter snake presence was not related to treefrog presence (χ^2_1 = 0.81, P = 0.367).

TABLE 259. Co-occurrence of garter snakes with trout, minnows, and treefrogs at 88 lentic sample units in the Lake Tahoe basin.

	Trout		Minnows		Treefrogs	
	Present	Absent	Present	Absent	Present	Absent
Garter snakes present	14	6	12	8	8	12
Garter snakes absent	21	47	17	51	33	35

Garter snakes were not detected on the north side, but the frequency of occurrence of garter snakes did not differ significantly among orientations (χ^2_3 = 5.76, P = 0.124).

Garter Snakes in Lotic Riparian Ecosystems

General Patterns

Thamnophis was the only taxa of amphibians or reptiles encountered frequently enough in lotic environments to analyze its environmental relationships. *Thamnophis* was detected on a total of 9 reaches (Table 260), with observations on 3 reaches only identified to genus. Two species of *Thamnophis* were detected: western aquatic garter snake (n = 2 reaches), and western terrestrial garter snake (n = 5 reaches) (Table 260).

TABLE 260. Garter snakes detected in surveys of lotic sample units (n = 80) in the Lake Tahoe basin.

Common name	Scientific name	Number of units	Frequency (%)
Western aquatic garter snake	*Thamnophis couchii*	2	2.5
Western terrestrial garter snake	*Thamnophis elegans*	5	6.3
Unidentified garter snake	*Thamnophis* sp.	8	10.0
All garter snakes	*Thamnophis* spp.	9	11.3

Environmental Relationships of Garter Snakes

Thamnophis presence was correlated with 8 environmental variables (Table 261). *Thamnophis* was positively correlated with channel width and sinuosity, meadow vegetation and lodgepole pine vegetation. *Thamnophis* was negatively correlated with elevation, channel gradient, mixed conifer vegetation, and canopy cover index.

TABLE 261. Significant ($P \leq 0.10$) correlations between *Thamnophis* presence and 22 environmental variables at sample reaches (n = 80) in the Lake Tahoe basin.

Environmental variable	*Thamnophis* presence	
	r	*P*
Abiotic environment:		
Elevation	-0.230	0.040
Channel characteristics:		
Gradient	-0.378	0.001
Width	0.291	0.009
Sinuosity	0.187	0.097
Vegetation characteristics:		
Meadow	0.285	0.010
Mixed conifer	-0.267	0.016
Lodgepole pine	0.432	<0.001
Canopy cover index	-0.374	0.001

The logistic regression model for abiotic environment consisted of 2 variables: a negative association with elevation and a positive association with precipitation (correctly classified: presence = 0%, absence = 100%) (Table 262). The poor prediction of presence based on elevation and precipitation was improved slightly with the addition of distance to stream mouth (correctly classified: presence = 11%, absence = 99%). The logistic regression model for channel characteristics consisted of a one variable model: a negative association with channel gradient (correctly classified: presence = 11%, absence = 99%) (Table 262). The poor prediction of presence based on channel gradient was improved slightly with the addition of channel width (correctly classified: presence = 22%, absence = 99%). The logistic regression model for live vegetation characteristics consisted of a 2 variable model: a negative association with canopy cover index and a positive association with lodgepole pine (correctly classified: presence = 22%, absence = 100%) (Table 262). The poor prediction of presence based on lodgepole pine and canopy cover index was much improved with the inclusion of all 9 live vegetation variables (correctly classified: presence = 67%, absence = 96%). This predictive model is just as feasible as the 2 variable model in a practical sense, given that it requires a commensurate amount of effort to describe one vegetation type as to describe all of them. No variables were selected in the regression model with woody debris. A backwards stepwise logistic regression of the 5 key variables selected in the individual regression models resulted in a 3 variable model: positive associations with lodgepole pine; and negative associations with canopy cover index and elevation (correctly classified: presence = 44%, absence = 97%) (Table 263).

TABLE 262. Logistic regression relationships between *Thamnophis* presence and 22 environmental variables at sample reaches (n = 80) in the Lake Tahoe basin. N = negative association, P = positive association with $P \leq 0.10$. Bolded indicates variable was selected in final regression model.

Environmental variable	*Thamnophis* presence
Abiotic environment:	
Elevation	**N**
Precipitation	P
Channel characteristics:	
Gradient	N
Vegetation characteristics:	
Lodgepole pine	**P**
Canopy cover index	**N**

TABLE 263. Final logistic regression model of key variables related to *Thamnophis* presence at sample reaches (n = 80) in the Lake Tahoe basin.

Variable	B	SE	Wald	ν	*P*	R
Elevation	-10.622	6.062	3.071	1	0.080	-0.138
Lodgepole pine	2.854	1.230	5.381	1	0.020	0.245
Canopy cover index	-0.047	0.021	4.844	1	0.028	-0.225

Two of the 5 variables selected in the regression models exhibited potential threshold levels. *Thamnophis* was not observed above 2100 m in elevation, although over 40% (n = 33) of all sample reaches were above 2100 m in elevation. *Thamnophis* was also not observed on sample reaches with over approximately 60% canopy cover index, although almost 40% (n = 31) of all sample reaches exceeded a 60% canopy cover index.

Thamnophis was observed on all sides of the basin (north, south, east, and west). However, 77.8% (n = 7) of all sightings occurred on the south and west sides of the basin. Based on the number of reaches, *Thamnophis* occupied 19.4% of the reaches on the south and west sides, whereas it only occupied 4.5% of the reaches on the north and east sides of the basin. ANOVA showed no differences in frequency of occurrence among the 4 orientations within the basin.

DISCUSSION

Brown-headed Cowbird

Cowbirds were detected more frequently than almost every other riparian–meadow bird and were in the top 20% of all birds. In the past 40 years, cowbirds have established populations in the basin and become fairly common. This trend is disconcerting because of the cowbird's potential to hinder the reproductive success of many of the basin's passerines.

We found that cowbirds were most abundant at low elevation sample units, at sample units near meadows, at east side sample units, and at highly disturbed sample units. These findings are in accordance with known cowbird natural history: they generally forage in open habitats, particularly near grazing animals (Granholm 1990), and they forage in areas of high human disturbance, especially where cattle graze or where pack stations have been established (Robinson et al. 1993). Increased cowbird abundance on the east side and at low elevations are likely results of human development being greatest there and grazing mammals being more frequent at low elevations.

Cowbird management may be warranted in the basin, but additional work needs to be done to better define the scope of the problem. Robinson et al. (1993) outline steps for managers when parasitism is suspected to have major impacts on other nesting passerines. Recommended steps include assessment of cowbird presence, density, and of patterns of occurrence, and determination of the degree to which parasitism affects species of concern, including effects on the reproductive success of hosts. If cowbird parasitism is shown to affect species of concern significantly, then cowbird management may be justified.

Methods used to control cowbirds can include trapping, shooting, landscape and habitat management, and livestock management (Robinson et al. 1993). Trapping is probably the most efficient and politically feasible methods of cowbird control; trapping specifics are given in Robinson et al. (1993). Cowbird trapping programs have been somewhat successful in reducing parasitism on certain listed species in other regions (Lowther 1993, Robinson et al. 1993). Shooting is also likely effective, especially along with trapping (Robinson et al. 1993), but may not be supported by the public. Landscape and habitat management are probably the most effective methods of long-term cowbird management; the primary objective is to maintain large areas of contiguous habitat while maximizing the habitat-to-edge ratio (Robinson et al. 1993). Finally, management of livestock and pack stations to reduce feeding opportunities for cowbirds may also reduce cowbird populations in the long term (Robinson et al. 1993).

Current management direction from the Tahoe Regional Planning Agency (TRPA) and the USDA Forest Service (USFS) may assist in deterring cowbird expansion in the basin. TRPA's Goals and Policies (1986) call for the control of exotic species; the cowbird can be considered an exotic species in this regard (S. Romsos, pers. comm.). The USFS's Sierra Nevada Framework Project (USDA 2000) has mandated several standards and guidelines that relate to Willow Flycatcher protection, including reducing grazing in occupied meadows, that will also reduce the threat of cowbird parasitism.

Beaver

Physical environmental characteristics had the strongest relationships with beaver presence. Beaver were present more frequently in low elevation, low gradient, wide reaches close to the mouth of streams. The absence of beaver on the north side of the basin is most likely a function of the high gradient, low sinuosity reaches on that side of the basin.

Vegetation associations indicate that beaver presence is associated with more open valley forms, as indicated by the association with meadow and lodgepole pine vegetation. Meadow and lodgepole pine are both associated with low-sloped terrain and typically occur within the floodplain of streams in the Lake Tahoe basin.

Beaver may be undesirable in the Lake Tahoe basin from an ecosystem conservation perspective. Because they are considered an exotic species, the environmental changes they induce may be outside the range of conditions produced by natural disturbance regimes such as woody debris recruitment into the stream and flooding regimes. Beaver increase the amount of woody debris in streams as a function of their life history, as reported elsewhere (Pollock et al. 1995) and evidenced in this study by the positive relationship between beaver and channel wood volume. In addition, beaver use the woody debris to increase the amount of ponded water near their den sites. The increased ponded water changes the character of the stream in that location, altering its suitability as habitat for a variety of biota.

The increased woody debris in the stream channel can dramatically change the sediment regime and the behavior of the channel during flooding events, sometimes creating major erosion and channel alteration (Pollock et al. 1995). Sediment regimes in high mountain streams may consist of a more continuous delivery of sediment without beaver. In streams with beaver, their dams capture and store sediment which then becomes liberated during high flow events, resulting in a sediment regime characterized by a more pulse delivery of sediment. The net sediment delivery from streams with beaver may be greater or lesser than those without beaver. Sediment delivery from streams to Lake Tahoe is of major concern because increased sediment delivery (and associated nutrients) to the lake is suspected to be one of the primary threats to the renown clarity of Lake Tahoe.

The management of beaver in the Lake Tahoe basin is complicated by numerous factors. First, beaver are common in the Lake Tahoe basin, observed in this study in over 50% of the watersheds sampled, and often observed on multiple reaches per watershed. Second, the management of the Lake Tahoe basin is of great interest to local and remote members of the public. Most members of the public enjoy seeing beaver, are interested in maintaining beaver populations in the basin, and do not support beaver population control measures. Relocation efforts between watersheds in the basin have been partially successful (J. Reiner, pers. comm.) but this approach to population management is effort-intensive because beavers often return to their home territories within the same year.

Efforts to reduce and remove beaver from some watersheds should probably concentrate on watersheds that are relatively ecologically intact (e.g., not dammed, no artificial channel alterations, relatively undeveloped) and that have suitable habitat for beaver. In the remaining watersheds, watershed conservation measures might include determining where beaver are doing the most damage to channel conditions and biota, and keeping populations in these watersheds at minimum levels. Beavers could be relocated to watersheds where their populations will be more resource limited, such as small sized watersheds with more narrow channel widths and higher gradient channels. Other management techniques, such as dam removal, may be effective in reducing the potential for ecological damage without moving or threatening the viability of individual or populations of beaver.

Amphibians

The basin's amphibians showed disparate environmental relationships. The varied patterns observed explain in part the poor predictive ability of the model generated for amphibian species richness and reported in Chapter 11. In addition, the differing patterns suggest that, generally speaking, habitat restoration targeted at a single amphibian species is unlikely to improve conditions for other amphibian species. However, most of the native amphibian species appeared to be limited by the presence of trout, based on evidence presented here and in other studies. Below, we discuss our findings for each species.

Pacific Treefrog

Treefrogs were detected at nearly one-half of all sample units and were by far the most frequent and abundant amphibian in our surveys. Treefrogs are known to occupy nearly every lentic ecosystem type in the Sierra Nevada (Morey 1988a), but in the basin we found clear patterns of occurrence. Treefrogs were more abundant at small, shallow sample units with silt substrates and plenty of littoral zone vegetation (also known as eutrophic, or high productivity, sites). Sample unit depth emerged as the primary environmental factor associated with treefrog abundance. However, Bradford (1989) detected no effect of depth on treefrog occurrence apart from an observed minimum. Treefrogs may have selected shallow sites for increased water temperature, which allows quicker metamorphosis (Bradford 1989), or they may be excluded from deeper sites by introduced trout. Eutrophic sites also may provide an abundance of food for treefrogs, while oligotrophic (low productivity) sites provide less food.

Although introduced trout have been implicated in the decline of some frogs (Hayes and Jennings 1986, Bradford 1989, Bradford et al. 1993, Knapp and Matthews 2000), trout are not suspected to restrict treefrog distributions. However, our data suggest that trout occurrence may limit treefrog occurrence in the basin. Trout may prey on treefrog adults, larvae, or eggs, although this has not been specifically documented. Alternatively, trout and treefrogs may simply have opposing environmental relationships, given that trout were more common at deep, oligotrophic sites. Whether the decreased abundance of treefrogs at deep oligotrophic sites is attributable to the presence of trout or to a preference for shallow productive sites could be determined by experiments. Such experimental work could yield an understanding of trout–frog relationships that would inform the management of treefrog populations in the basin.

Western Toad

Few environmental relationships of western toads were revealed by this study, in part because of the low number of toad detections. Toads were associated with a range of elevations and substrate characteristics, consistent with their characterization as habitat generalists (Morey 1988b). However, toads were detected only at sample units larger than 2 ha, which was well above the median area of sample units (0.97 ha). A relationship between toad occurrence and lentic unit area has not previously been reported. In addition, we found that toads were more frequent at sample units surrounded by subalpine conifer vegetation. This pattern is not likely attributable to an association with higher elevations, as western toads occur at a wide range of elevations in California (Morey 1988b), and we did not find that toad occurrence was related to elevation. Therefore, it is likely that this result is an artifact of the small sample, and would not persist with a greater number of detections. Finally, trout were present at 7 of the 8 sample units with toads. The apparent association of toads with trout likely reflects similar habitat associations rather than some interaction among these species.

Toads were relatively uncommon across sample units. Toads are generally considered common throughout the state (Morey 1988b), and are not suspected to be negatively affected by direct human disturbance or exotic fish, factors that may influence the distributions of other amphibians in the basin. Given that toads are readily detected with the methods we employed, it appears that toads are truly rare in this area. Their rarity may be attributed to the basin being toward the upper end of their elevational range (Morey 1988b).

Long-toed Salamander

No environmental variables had significant relationships with long-toed salamander occurrence, perhaps due to the low detection rate of salamanders. One pattern suggested by the data is that salamanders rarely persist at sample units with trout. Edgewood Lake was the only sample unit where we detected both salamanders and trout, and only 2 salamander larvae were detected, 1 of them dead. There were too few detections of salamanders in our study to yield a statistically significant result, but the pattern of non-overlap between salamanders and trout fits emerging information about long-toed salamander habitat relationships. Ambystomatids such as long-toed salamanders may be unable to coexist with trout, a relationship shown in field studies in other regions (Tyler et al. 1998) and suggested to occur in the basin (Schlesinger and Holst 2000). Trout prey on long-toed salamander larvae (Tyler et al. 1998, Basey and Morey 1988) and have apparently extirpated salamanders from some areas in the Sierra Nevada (B. Shaffer, pers. comm.). In the basin, it appears that salamanders may have been extirpated from most permanent waters by trout, relegating salamanders to temporary ponds. Such ponds, especially those at higher elevations, often dry up before metamorphosis is complete, thereby killing the remaining larvae. Further, the potential absence of salamanders from permanent waters suggests that critical source populations of salamanders may have been lost in the basin (B. Shaffer, pers. comm.). Studies that examine the relationship of pond permanence, trout presence, and salamander occurrence are needed in the basin.

No native salamanders have been detected in Nevada before this survey (R. Espinoza, pers. comm.). Thus, the detection of long-toed salamanders at Edgewood Lake is a significant finding—the first record of native species of the vertebrate order Caudata in Nevada. This detection does not constitute a major range expansion for the species, but rather a discovery that salamander populations extend across the California–Nevada border in the basin. It is not surprising that salamanders were found on the Nevada side of the basin, because the basin is one of the few places where Sierra Nevada ecosystems occur in Nevada, and the salamander's range was known to extend to near the border (Behler and King 1979, Stebbins 1985). Furthermore, we found salamanders at 2 additional lentic units (Hell Hole and Sky Meadows Pond) near the Nevada border on Lake Tahoe's south shore. This evidence suggests that long-toed salamanders are likely to exist at multiple sample units in Nevada near the California border in the basin. Further surveys are needed to define the species' range in Nevada.

We sampled many environments seemingly suitable for salamander breeding, so it is surprising that salamanders were detected so infrequently. We did not detect more than 5 larvae at any sample unit, suggesting that salamanders might often occur in small numbers, hindering their detection. Additional detections of salamanders are necessary to validate the patterns suggested by our data. Further, more basin-wide surveys are needed to assess the status of the species in the basin.

Bullfrog

We detected bullfrogs at 4 sample units, all of them occurring at lower elevations on the south side of the basin in areas of high human development and visitation. We found bullfrogs up to 2030 m, higher than the maximum elevation reported by Morey (1988d). The sample units generally contained little silt and an abundance of sand and pebbles. Bullfrogs were detected at too few sample units for environmental relationships to be determined statistically, but the association of bullfrogs with low elevation and high human disturbance was indicated. Bullfrogs do exist at some sites in the Sierra Nevada that are far from human development (pers. obs.), but in the basin they may be restricted from dispersing far from human settlement because areas uninhabited by people lie above their elevational limit.

If populations of bullfrogs continue to expand to a greater proportion of low elevation sample units, they could pose a growing threat to native species. It is likely that bullfrogs have already reduced or eliminated populations of native amphibians, snakes, invertebrates, and fish in some occupied sites in the basin, given the general trends observed in other studies (e.g., Moyle 1973, Hayes and Jennings 1986). Studies determining the extent of bullfrog distribution in the basin and identifying areas at greatest risk of invasion need to be conducted. For example, bullfrogs at the 2 lentic units closest to undeveloped areas (Fallen Leaf Lake and Seneca Pond) are of primary concern, as these sites represent potential starting points for expansion into Desolation Wilderness.

Bullfrog control may not be warranted at this time, but if bullfrogs begin to threaten species of concern, such as the mountain yellow-legged frog or Lahontan Lake tui chub (*Gila bicolor pectinifer*), control should be considered. However, some residents enjoy having the frogs in their backyards (pers. obs.), so a balance between ecological and cultural interests will be necessary.

Mountain Yellow-legged Frog

We detected mountain yellow-legged frogs at 2 lentic units in the basin; to our knowledge, our observations of larvae at both lentic units constitute the only records of yellow-legged frog breeding in the basin in several decades. Surveys for additional occupied sites are needed. We have made informal visits to both sites since our initial surveys, detecting no mountain yellow-legged frogs at Skinny Whale Pond but finding a substantial population at Hell Hole, consisting of hundreds of tadpoles, many juveniles, and at least 3 adults. Both sites appear to be suitable mountain yellow-legged frog habitat because they are permanent water bodies with a depth of at least 2 m in some places and have no trout, critical habitat features for mountain yellow-legged frog breeding populations.

Trout appear to be the biggest factor in the decline of the mountain yellow-legged frog in the Sierra Nevada (Knapp and Matthews 2000). The frog's susceptibility to predation by trout may be due to the 1½ to 2½ years it takes tadpoles to achieve metamorphosis (Bradford et al. 1993). Most of the formerly fishless waters of the basin now contain exotic trout (Elliott-Fisk et al. 1997), drastically limiting suitable habitat for mountain yellow-legged frogs. The 2 lentic units where we located mountain yellow-legged frogs were both free of fish. Hell Hole lies in a fishless drainage (J. Reiner pers. comm.), and Skinny Whale Pond appeared to be isolated from lakes with fish, despite a small stream connecting the pond to Upper Velma Lake, which contains trout (Schaffer 1998). Although some other sample units were deep enough for mountain yellow-legged frog breeding and lacked trout, they may be isolated from source populations of frogs by lentic units with trout.

The persistence of mountain yellow-legged frog populations in the basin appears to be at risk, with only a single known population. Small, isolated populations of mountain yellow-legged frogs are at risk of extirpation due to stochastic environmental and demographic events (Bradford et al. 1993) as well as inbreeding and the risk of trout somehow being introduced. A network of sites allowing movement of frogs among sites would increase the probability of persistence. Additional sites may need to be colonized, possibly by reintroduction, coupled with eradication of exotic trout from some sites.

Reintroduction of mountain yellow-legged frogs would need to be carefully considered. Reintroductions of species of concern commonly have low success rates, and mountain yellow-legged frog reintroductions have been attempted unsuccessfully in other parts of the Sierra Nevada (G. Fellers pers. comm.). The appropriate considerations in site-selection for mountain yellow-legged frog reintroductions have not been carefully studied, but most likely would include presence of suitable habitat, historical frog presence, absence of exotic trout and bullfrogs (or the possibility of eradication), lack of connection to streams or lakes with trout or bullfrogs, no or minimal recreation pressure, and no or minimal livestock grazing. The prevalence of exotic trout in Desolation Wilderness and the ease of movement for trout up and down most streams would probably necessitate that entire drainages be devoted to frogs, with fish populations eradicated. One study has shown that fish populations can be eradicated from some alpine lakes containing mountain yellow-legged frogs (Knapp and Matthews 1998) with the result that frogs dramatically increased in abundance shortly thereafter (Knapp and Matthews 2000). Eradicating trout from entire drainages is a complex issue given the strong interest in sport fishing in the basin, and is likely to be expensive. However, such a measure may well be necessary for the conservation and restoration of mountain yellow-legged frogs in the basin.

Garter Snakes

Small sample sizes and restricting the analysis to the genus level limits the discussion of ecological relationships to general observations and potential interactions. However, given the strength of the relationships observed, we would expect them to remain consistent with additional sampling.

In lentic ecosystems, garter snakes were most frequently associated with larger, deeper lakes with rocky substrates, abundant logs, fish, and sparse littoral zone vegetation. Garter snakes occurred more frequently in association with fish, suggesting that fish are a primary prey item, as others have reported (Fitch 1941, Zeiner et al. 1988, Rossman et al. 1996). This pattern could be further investigated in the basin with a dietary study. Snakes are known to prey on frogs (Fitch 1941), but the disparate environmental relationships shown by garter snakes and treefrogs suggests that treefrogs may not be a primary prey item of garter snakes in lentic habitats in the basin. Garter snake diets can be quite diverse, including terrestrial small mammals and amphibians (Fitch 1941).

No direct relationship between garter snake presence and elevation was apparent in lentic ecosystems, despite the positive relationship between garter snakes and precipitation and rocky substrates (which were highly correlated with elevation). However, garter snakes were absent from the highest elevation lentic sample units, and they were observed significantly less frequently at higher elevation lotic sample sites. The maximum elevation at which we found garter snakes was 2565 m (at Meiss Lake), but western terrestrial garter snakes are known to occur up to 3660 m (Morey 1988e). We did detect western aquatic garter snakes at 2536 m, higher than the 2400 m reported by Morey (1988f). Absence of suitable prey does not appear to have prevented garter snakes from occupying those sample units—of the 7 sample units with elevations higher than 2565 m, 4 contained either fish or treefrogs. Possibly, maximum elevations reported have been recorded at lower latitudes in the Sierra Nevada, where environmental conditions are less extreme. Indeed, garter snakes appeared to be more frequent in warmer environments, particularly in association with lotic ecosystems. Lower elevations are warmer, and meadow and lodgepole pine are the most open-canopied vegetation types at lower elevations, allowing more solar radiation to reach the ground. The south and west sides of the basin also generally receive the more solar radiation that the other 2 orientations in the basin.

Garter snakes appeared to be more frequent in open canopied, mesic environments and larger water bodies, be they lotic or lentic. Canopy cover is a condition readily influenced by management, and consideration of vegetation management along streams should consider influences on garter snake habitat suitability. Further, a greater association with south and west orientations in lotic environments indicates that these more mesic environments constitute more suitable habitat for these water-associated garter snakes. The higher canopy cover on the north and east sides is likely to be directly related to the smaller width streams on these basin orientations. The larger streams on the south and west sides, along with the greater proportion of lodgepole pine on the south and west sides. Larger streams are also likely to have a greater abundance of food resources, fish in particular, and the grassy understory of lodgepole pine is amenable to the terrestrial movements.

The abundance of various vegetation types was not associated with garter snake occurrence in lotic ecosystems, but it was strongly associated in lotic ecosystems. In lotic ecosystems, garter snakes were most frequently associated with lower elevation areas with low canopy cover and lodgepole pine vegetation. Predictive capabilities of the model are likely to improve further with the inclusion of all vegetation types and precipitation (identified in the individual regression models), and the inclusion of these data would not require any additional data collection or analysis time. Thus, these key variables could be as the basis of a habitat suitability model for garter snakes in lotic habitats.

All of the variables selected in the final regression model for lotic habitats are readily available from remotely sensed data and existing GIS maps. However, only a few of the variables selected in the lentic model are readily available from existing maps, namely precipitation, area, and depth. Additional surveys should be conducted to increase the sample size for lotic and lentic ecosystems before any habitat suitability model is created for use in making management recommendations or decisions. However, with additional survey results, potential habitat for garter snakes in lotic and lentic riparian areas could be modeled throughout the basin based on variables available from existing GIS maps, and the results, combined with similar models for other species of concern, could be used as prior information in project planning, and could be used to derive a conservation strategy for riparian-associated species of concern throughout the basin. Once the model is built, a modest field effort consisting of field visits to a random sample of sites could be conducted to validate and strengthen the accuracy of model predictions.

This project represents the first probabilistic survey of the basin's garter snakes to our knowledge. Garter snakes are generally poorly studied in the Sierra Nevada, although some past studies (e.g., Fitch 1941) established basic habitat relationships and some ongoing field surveys (e.g., G. Fellers, pers. comm.) should further refine knowledge of patterns of garter snake occurrence and their habitat relationships. The western terrestrial and western aquatic garter snakes are identified as species of concern in the Lake Tahoe basin (Manley et al. 2000), and further research would be useful to elucidate patterns of occurrence and differences in habitat associations among the basin's 3 species. Management of lentic and lotic environments to enhance habitat suitability for garter snakes should be directed toward sites below 2100 ft in elevation and on the south and west sides of the basin.

NEXT STEPS

The Lake Tahoe Watershed Assessment provided a valuable synopsis of species and ecosystems of concern in the basin. The species selected here for individual analysis constitute a small set of species known to have impacts on riparian biota or for which richness calculations were infeasible. The potential exists to develop habitat relationships models for high priority focal species associated with riparian environments. These models would provide valuable species-specific data for management of populations in the basin. Perhaps more importantly, they could also be used to identify priority management and conservation areas for individual species and riparian biodiversity. Such models would constitute a fine-filter complement the 'meso-filter' models of riparian species richness and the coarse-filter model of community diversity and ecologically significant areas portrayed in the Lake Tahoe Watershed Assessment.